THE *PHYSOSTEGIA PURPUREA-LEPTOPHYLLA-DENTICULATA* PROBLEM: TAXONOMIC AND NOMENCLATURAL CLARIFICATION

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There is much disagreement among floristic works about the taxonomic status of the obtusely-toothed to entire-leaved species of *Physostegia* that occur on the Atlantic and eastern Gulf Coastal Plain from southeastern Virginia to Florida (Figure 1). Ahles (1964) treated the complex as a single species (incorrectly placed in the genus *Dracocephalum*, a name that has been conserved for a different genus), but earlier authors (Elliott, 1816–1824; Small, 1913, 1933; Fernald, 1950) recognized two to three species. The confusion has been compounded by nomenclatural disagreements, at least eight epithets having been applied to members of this complex in major floristic works.

My own studies of the group, undertaken in connection with a systematic study of the genus as a whole, indicate that the complex consists of three species. One of them, *Physostegia godfreyi* Cantino, is easily distinguished and has been discussed elsewhere (Cantino, 1979); it will not be considered here. The other two species, *P. purpurea* (Walter) Blake and *P. leptophylla* Small, overlap somewhat morphologically but differ in habitat requirements and chromosome number. They are nearly to completely reproductively isolated from each other. In the following discussion, systematic and nomenclatural aspects of the problem will be discussed separately.

SYSTEMATICS

Physostegia purpurea and *P. leptophylla* differ in six morphological characters, but in each of these characters the ranges of character states found in the two species overlap. The four most discriminating characters have been plotted on a scatter diagram (Figure 2). Two characters, corolla color and shape of the leaf apex, have been omitted from the diagram.The corollas of *P. purpurea* tend to be a paler pink than those of *P. leptophylla,* but the difference is difficult to quantify, and the interspecific overlap is at

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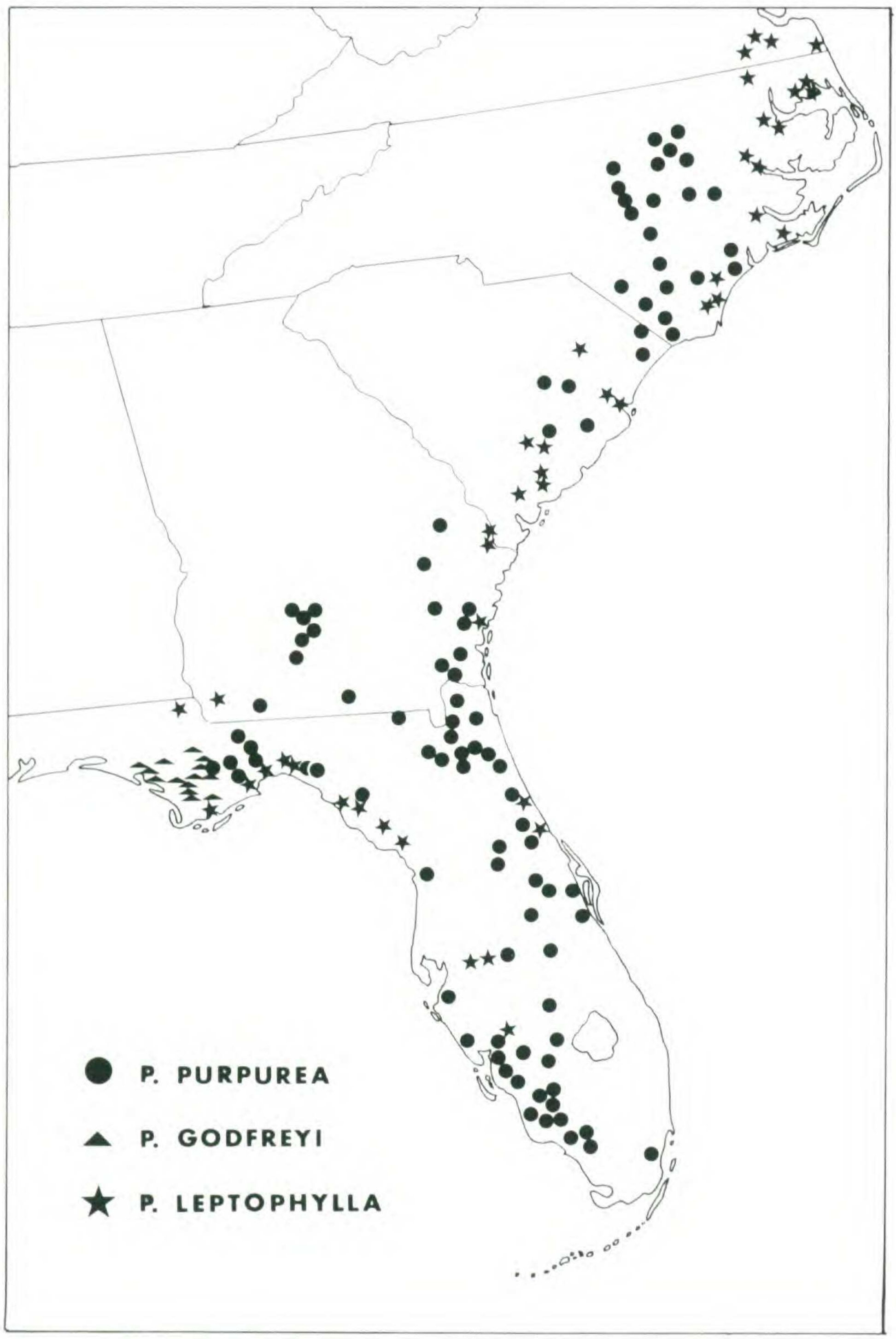

Figure 1. **Distribution of Physostegia purpurea, P. leptophylla, and P. godfreyi.**

least as great as in any of the characters included in Figure 2. The leaf apex, which tends to be obtuse in *P. purpurea* and acute to attenuate in *P. leptophylla*, is a fairly reliable diagnostic character in the northern part of the range of the two species but is of little use in Florida, where the leaves of *P. purpurea* are frequently so narrow that the genes responsible for an obtuse apex cannot be expressed—the leaf apices are automatically acute.

Of the characters included in Figure 2, by far the most discriminating is the degree of reduction of the upper stem leaves (vertical axis), expressed as a ratio of the length of the leaves of the second pair below the terminal receme to the length of the internode directly above them. There is considerably more overlap in the number of lower nodes bearing petiolate leaves (horizontal axis), the form of the rhizome (shading of the circles), and the shape of the leaves (projections from circles). The degree of overlap in the lattermost character is not immediately obvious from the diagram. In 82% of the specimens of *Physostegia purpurea* there is at least one leaf widest above the middle of the blade, versus 13% of the specimens of *P. leptophylla*. In contrast, 62% of the specimens of *P. leptophylla* have at least one leaf widest below the middle of the blade, versus 8% in *P. purpurea*. In spite of the fact that there is interspecific overlap in every character, the data points form two obvious clusters, particularly if the three specimens represented by the points labeled "A" and "B" in Figure 2 are excluded. These three specimens could not be placed in either species on the basis of morphology alone; their identification is discussed below.

The sample of herbarium specimens upon which the scatter diagram was based was not entirely random. The sample of *Physostegia leptophylla* was unbiased (at least to the extent that herbarium specimens ever provide an unbiased sample), in that all of the specimens at my disposal that included the necessary structures were used. However, the sampling of *P. purpurea*, of which a much greater number of specimens was available, was biased towards the inclusion of the widest possible range of variation in the characters of interest. Thus the degree of morphological overlap is exaggerated in Figure 2; the relative frequency of specimens of *P. purpurea* exhibiting one or more character states that can also be found in *P. leptophylla* is somewhat higher than if the sample had been random.

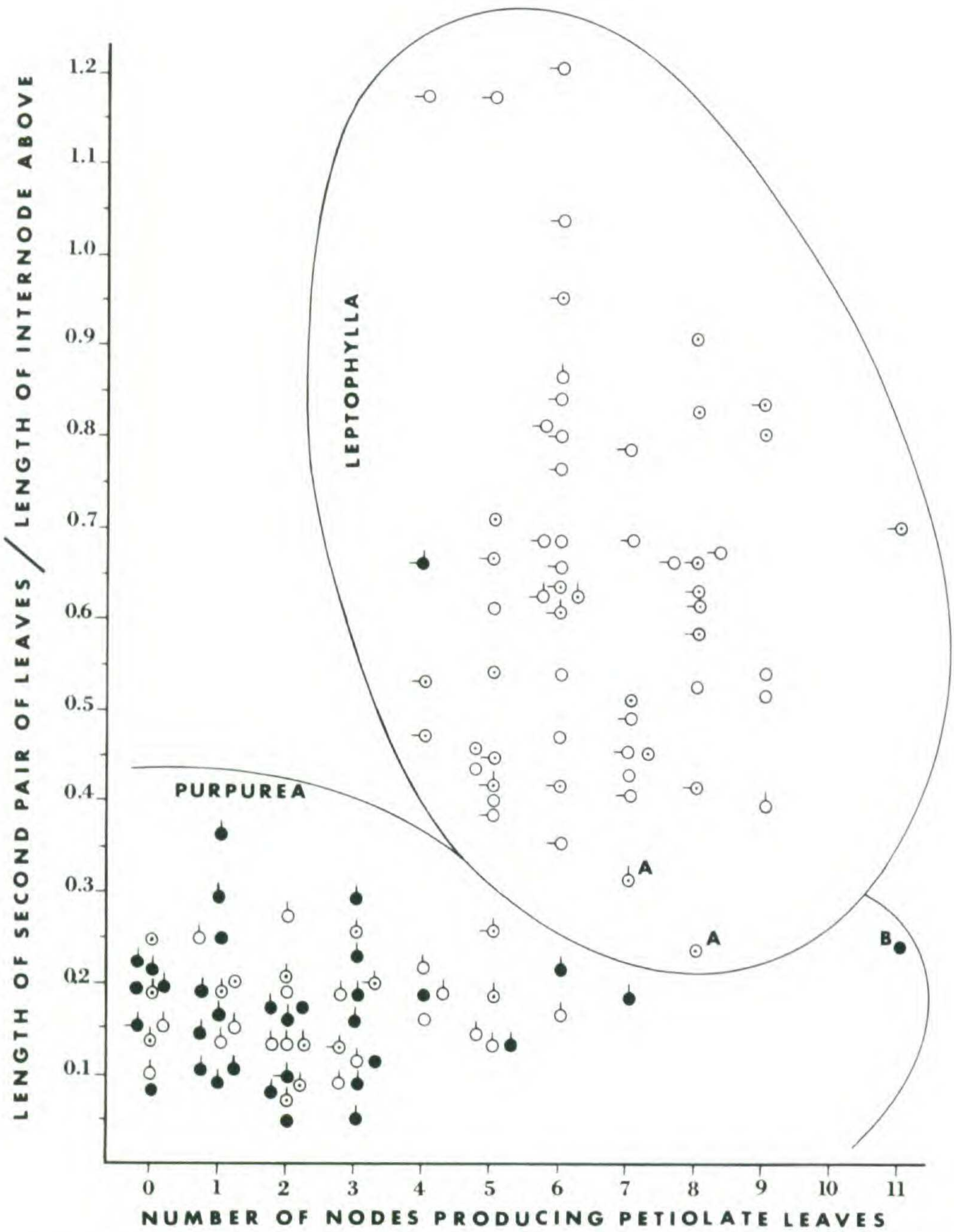

Figure 2. **Morphological overlap between Physostegia purpurea and P. leptophylla.**

Each point represents a single herbarium specimen. Shading of circles: clear circle, horizontal rhizomes present on specimen; blackened circle, no horizontal rhizomes produced by the plant; circle with dot in center, underground parts missing from specimen (rhizome unknown). Projections from circles: upwards if at least one leaf on specimen widest above middle of blade; to the side if at least one leaf on specimen widest below middle of blade; both upwards and to the side if specimen includes leaves widest above middle of blade and leaves widest below middle; no projections if all leaves widest near middle of blade. A, B: see text.

Table 1. **Chromosome Numbers of Physostegia purpurea and P. leptophylla**

Physostegia purpurea

Chromosome Number ($2n$)	Location of Population	Voucher (GH)
38	North Carolina: Nash Co., 1 mi E of Middlesex	*Cantino 935*
38	North Carolina: Harnett Co., 3 mi SE of Bunnlevel	*Cantino 939*
38	Georgia: Turner Co., ca 8 mi W of Irwinville	*Cantino 1034*
38	Florida: Collier Co., E of Ochopee	*Cantino 1142*
38	Florida: Wakulla Co., 8.4 mi WNW of Sopchoppy	*Cantino 1143*

Physostegia leptophylla

Chromosome Number ($2n$)	Location of Population	Voucher (GH)
76	Virginia: Southampton Co., Zuni	*Cantino 970*
76	North Carolina: Pitt Co., ca 6 mi WNW of Washington	*Cantino 973*
76	South Carolina: Georgetown Co., Sampit	*Cantino 982*
76	Florida: Taylor Co., 2.8 mi S of Tennile	*Cantino 1140*
76	Florida: Wakulla Co., 2 mi SW of Wakulla	*Cantino 1141*

The chromosome numbers of *Physostegia purpurea* and *P. leptophylla* have never before been reported. Root tips, obtained from greenhouse plants which had been raised from rhizomes collected previously in natural populations, were used to determine the mitotic numbers of these species. The root tips were pretreated in 8-hydroxyquinoline and then dissected in aceto-orcein, according to the procedure outlined by B. W. Smith (1974; pp. 251–252), originally adapted from Tijo & Levan (1950). The results (Table 1)

indicate that *P. purpurea* has 38 chromosomes, the number found in most species of *Physostegia* (Cantino, in press), whereas *P. leptophylla* is a tetraploid with 76 chromosomes.

Physostegia leptophylla and *P. purpurea* are reproductively isolated by means of several partially effective mechanisms which are superimposed on one another like a set of sieves with progressively finer meshes. The first level of isolation is ecological. In spite of their extensive sympatry (Figure 1), I know of no instance of the two species occurring at the same site. They have markedly different habitat requirements. *Physostegia leptophylla* is found in wooded river swamps and in fresh and brackish marshes. It frequently grows in shallow water and can tolerate deep shade. *Physostegia purpurea* is a species of open pinelands, where it is generally found in moist sites but usually not in standing water. It rarely grows in the shade and never in deep shade.

Ecological isolation is undoubtedly very effective in restricting the opportunities for hybridization between the two species, but the habitats to which they are confined can be found adjacent to one another, a situation that might permit occasional insect-mediated pollen transfer. If this were to occur, two postzygotic barriers to gene flow would come into operation—seed-incompatibility and hybrid sterility.

Experimental crosses between *Physostegia purpurea* and *P. leptophylla* failed to yield any mature seed, although intraspecific crosses involving each species were sucessful (Table 2). Eight geographically scattered populations of *P. purpurea* and seven of *P. leptophylla* were represented among the parent plants in the interspecific crosses. Percentage figures in Table 2 are based on a maximum yield of four nutlets per flower pollinated. Nutlet initiation was scored a few days after the pollinations were carried out by counting the number of ovary lobes that had begun to enlarge; each ovary lobe can potentially develop into a single-seeded nutlet. Further details of the study are presented elsewhere (Cantino, in press).

In the interspecific crosses, nutlets were initiated but they aborted before reaching maturity, a result that indicates that the breeding barrier is postzygotic. It is not known whether this isolating mechanism is as effective under natural conditions as it is in the experimental garden. In the event that an occasional hybrid seed were to be produced in nature, in spite of the ecological isolation of

Table 2. **Results of controlled pollination experiments involving Physostegia purpurea and P. leptophylla**

	Number of Trials (Pairs of Plants)	Total Number of Flowers Pollinated	Percent Nutlet Initiation	Percent Nutlet Maturation
Purpurea × Purpurea	5	60	60.4%	41.3%
Leptophylla × Leptophylla	5	93	73.9%	54.8%
Leptophylla (♂) × Purpurea (♀)	6	77	68.2%	0.0%
Purpurea (♂) × Leptophylla (♀)	5	57	81.6%	0.0%

the two species and the likelihood of seed abortion, the resulting plant would be triploid and therefore mostly sterile. Although none of the three isolating mechanisms, by itself, is completely effective, with the possible exception of the seed abortion observed in the garden, the combination of the three mechanisms could be expected to result in virtually total reproductive isolation.

I have seen no clear evidence of natural hybridization between *Physostegia purpurea* and *P. leptophylla*. A few specimens from Florida exhibit an intermediate morphology, but there is little evidence to suggest that they are hybrids rather than extremes in a pattern of overlapping interspecific variation. One of them (represented by point "B" in Figure 2) was collected from a population in Collier County, Florida (voucher: *Cantino 1025*), the other members of which had the characteristic morphology of *P. purpurea*. One member of the population (but not the intermediate specimen itself) was found to have 19 pairs of chromosomes, in agreement with other counts for *P. purpurea*. Because the nearest known occurrence of *P. leptophylla* is about 100 miles to the north, it is unlikely that the population is a hybrid swarm. It is far more plausible that the specimen represented by point "B" is simply a somewhat aberrant individual of *P. purpurea*.

A second instance of intermediacy between *Physostegia leptophylla* and *P. purpurea* was found in Taylor County, Florida (voucher: *Cantino 1026*). The plants were growing in a rocky stream bed, not a characteristic habitat for either species, and the morphology of various members of the population ranged from that which is usual in *P. leptophylla* to forms intermediate between *P. leptophylla* and *P. purpurea*. The most intermediate specimens are represented by the two data points labeled "A" in Figure 2. The single member of the population for which a chromosome count was obtained (not one of the most intermediate specimens) had 38 pairs, the number found in *P. leptophylla*. Lacking chromosome counts for the intermediate specimens, one cannot rule out the possibility that they are hybrids. However, I saw no *P. purpurea* growing in the vicinity, leading me to suspect that they are just aberrant individuals of *P. leptophylla*.

NOMENCLATURE

Of the specific epithets that have been applied to either *Physostegia purpurea* or *P. leptophylla*, three (*purpurea, incarnata,* and *denticulata*) are particularly problematical. These will be discussed in chronological order.

In his *Flora Caroliniana* (1788), Thomas Walter described three new species of what he thought to be *Prasium*. His uncertainty about their true affinities was evidenced by his placement of a question mark after the generic name, so that it appeared as "*Prasium?*". Soon after the publication of *Flora Caroliniana,* several botanists realized that Walter's *Prasium? purpureum* and *Prasium? incarnatum* were representatives of *Physostegia,* then known as *Dracocephalum*. Ventenat (1801) listed *Prasium incarnatum* in synonymy with his *Dracocephalum variegatum,* and Elliott (1816–1824) synonymized *Prasium purpureum* under *Dracocephalum denticulatum*. A century later, Blake (1915) examined the two specimens labeled as *Prasium* in the Thomas Walter Herbarium at the British Museum (Natural History) and verified that they were indeed *Physostegia*.

The typification of new names in Walter's *Flora Caroliniana* presents a problem in that there is no evidence that Walter actually based his descriptions on, or even saw, the collection of fragmentary material that is now regarded as the Walter Herbarium. Ward

(1977) discussed the situation in considerable detail. The relevant facts are as follows: John Fraser, who collected extensively in the southeastern United States in the late 1700's, returned to England in 1788, carrying with him the manuscript of Walter's *Flora Caroliniana*. Fraser also brought to England a collection of plant material which he claimed included specimens of the species in Walter's *Flora Caroliniana*, but he never claimed to be carrying Walter's herbarium. The origin of the folio of specimens in the British Museum that has generally been regarded as the Walter Herbarium is uncertain. Ward (1977) believes it likely that "A large but inferior collection of plants was gathered by Fraser during his travels, part or all of which may have been shown to Walter, and from which at a later date some other person, perhaps Fraser's son, selected specimens he believed representative of those species treated in *Flora Caroliniana*. This selection now constitutes the British Museum's 'Walter Herbarium.'" No other remnant of Walter's collections is known to exist. The Walter Herbarium does not circulate, but the entire collection was photographed by Bernice G. Schubert in 1946 and 1947, and the resulting album is available for study in the library of the Harvard University Herbaria.

Walter's short descriptions shed little light on the identity of the specimens upon which he based the names *Prasium? purpureum* and *Prasium? incarnatum*. There are two species of *Physostegia* that occur commonly in coastal South Carolina where Walter lived and collected, and both are variable enough in the characters used by Walter to distinguish *Prasium? purpureum* and *P. incarnatum* to preclude definitive association of either of Walter's names with either species on the basis of the descriptions alone.

Of the two specimens labeled as *Prasium* in the Walter Herbarium, Blake (1915) states that "The right-hand specimen, with sharply mucronate-serrate lanceolate leaves, which agrees with Walter's description of his *Prasium? incarnatum*, is *Physostegia virginiana* (L.) Benth., while the other, with linear-lanceolate crenate-dentate leaves, typifies *Prasium? purpureum* Walt. and is the same as *Physostegia denticulata* (Ait.) Britton." Blake accordingly labeled the two specimens in the Walter Herbarium as *Prasium? purpureum* and *P. incarnatum*. This constitues a lectotypification even though it is not known whether Walter actually saw the specimens in the "Walter Herbarium." Blake was

apparently not aware of this complicating factor, and it is clear from the introductory notes in his 1915 paper that it was his intention to link Walter's names with specimens in what he considered to be Walter's herbarium.

As will be shown later, Blake was probably incorrect in surmising that Aiton's *Dracocephalum denticulatum*, the basionym of *Physostegia denticulata*, was based on a type that is conspecific with the specimen labeled by Blake as *Prasium? purpureum* in the Walter Herbarium. But more importantly, he was clearly incorrect in stating that the right-hand specimen in the Walter Herbarium (which is indeed *Physostegia virginiana*) agrees with Walter's description of *Prasium? incarnatum*. Walter described *P. incarnatum* as having subamplexicaulous leaves and even italicized the word, presumably to emphasize its importance as a distinguishing character. The specimen that Blake labeled as *Prasium? incarnatum* in the Walter Herbarium has only two leaves, both of which are sessile but not amplexicaulous. Moreover, *Physostegia virginiana*, the species to which the specimen clearly belongs, practically never has anything approaching subamplexicaulous leaves. Blake's typification should, therefore, be rejected, leaving the name *Prasium? incarnatum* without a type. Inasmuch as it is impossible to determine from the description alone to which of two species (*Physostegia purpurea* or *P. leptophylla*) the name should refer, *Prasium? incarnatum* should be left as a *nomen dubium*.

It can perhaps be argued that both of Walter's names should be rejected as *nomina dubia* and more recent names applied to the two species of *Physostegia*. However, in view of the widespread and unambiguous use of the epithet *purpurea* in this genus, and the fact that the specimen in the Walter Herbarium that Blake labeled as *Prasium? purpureum* agrees with Walter's description, I believe it preferable to accept Blake's typification of *Prasium? purpureum*, thus retaining a long-standing name and avoiding confusion that would otherwise result.

In 1789, only a year after the publication of Walter's *Flora Caroliniana*, the name *Dracocephalum denticulatum* Aiton was published in *Hortus Kewensis*, based on a garden plant grown in England from material brought there from "Carolina" two years earlier. The type specimen, a photograph of which has been supplied to me by the British Museum, has proved to be perplexing. It

resembles certain specimens of *Physostegia virginiana* from Pennsylvania and West Virginia, but its leaf serrations are unlike those of the forms of *P. virginiana* that occur in the Carolinas. It is of course possible that the seed or rhizome from which the English garden plant was grown was sent from the Carolinas but collected elsewhere. A second, less likely possibility is that the specimen represents a somewhat aberrant individual of *P. purpurea*. The type specimen of *D. denticulatum* has much less reduced upper leaves than does *P. purpurea*, and it differs from the forms of *P. purpurea* that occur in the Carolinas in having acute, rather than obtuse, leaf tips. The former of these differences is of particular importance, because the striking reduction of the upper leaves in *P. purpurea* is its most distinctive trait.

One bit of evidence that suggests that the affinities of the type of *Dracocephalum denticulatum* lie with *Physostegia virginiana* rather than with *P. purpurea* is its blooming period. In the protologue of *D. denticulatum*, it is recorded that the plant blooms in August. In the Carolinas and neighboring states, *P. virginiana* blooms from mid-June through mid-October, with the majority of the plants blooming in July and August. *Physostegia purpurea* blooms in the Carolinas from late May through (rarely) the first few days of August, with the majority of the plants blooming in June.

Yet another bit of evidence suggesting affinity with *Physostegia virginiana* rather than *P. purpurea* comes from Curtis' *Botanical Magazine* (6: *tab. 214.* 1793), where a picture of *Dracocephalum denticulatum* was published only four years after the original publication of the name. The illustration is accompanied by the description drawn from *Hortus Kewensis* and by some additional notes, among which is a statement that the illustration is based on a plant grown from seeds collected in the vicinity of Philadelphia and is of the same species as the plant obtained by a Mr. Watson, an English nurseryman, from Carolina. The latter was apparently the garden plant upon which the original description in *Hortus Kewensis* was based. William Curtis and William Aiton were contemporaries in the London botanical community, so it is quite possible that Curtis actually saw living specimens of the plants Aiton described as *D. denticulatum*. Thus Curtis' statement that the plant illustrated in his magazine, which is clearly a representative of *Physostegia virginiana*, is of the same species as the one obtained

from Carolina lends support to the premise that the Carolina plant, too, was a form of *P. virginiana*.

On the basis of the evidence discussed above, I consider *Dracocephalum denticulatum* to be a synonym of *Physostegia virginiana*. The epithet *denticulatum* has, however, been applied to both *P. purpurea* and *P. leptophylla* (Small, 1913; Fernald, 1950), as well as to *P. virginiana* (Elliott, 1816–1824). The name should thus probably be rejected as ambiguous. Even if I am incorrect in my judgment about the affinities of the type specimen of *D. denticulatum*, and it actually represents an unusual form of *P. purpurea*, the name is still a later synonym and thus should not be applied to that species.

Fernald's use of the name *Physostegia denticulata* (Ait.) Britt. to represent *P. leptophylla* in Gray's Manual (1950) was based (Fernald, 1943) on his judgment that Aiton's brief diagnosis of *Dracocephalum denticulatum* corresponded well to plants Fernald had collected in Virginia (which fall within *P. leptophylla* as delimited here), together with the fact that the garden plants upon which the name was based were stated in the protologue to have come from "Carolina," where plants similar to Fernald's Virginia specimens abound. He apparently overlooked the fact that Aiton's diagnosis is equally descriptive of a number of other species of *Physostegia*. He makes no mention of having seen Aiton's type specimen, which is clearly not a representative of *P. leptophylla*.

Adding to the confusion, Chapman described in 1860 a var. *denticulata* of *Physostegia virginiana* without any reference to any earlier use of the epithet. The type specimen is unknown and the description is insufficient to determine whether the name was based on a specimen of *P. leptophylla*, *P. purpurea*, or *P. godfreyi*. Because there is no earlier use of the epithet at the varietal level, the name is legitimate, but unless a type specimen emerges, it is best left as a *nomen dubium*.

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